# Projected Effects of Climate Change on Patterns of Vertebrate and Tree Species Richness in the Conterminous United States

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## ABSTRACT

General circulation models (GCM) predict that increasing levels of atmospheric carbon dioxide ($CO_2$) and other greenhouse gases will lead to dramatic changes in climate. It is known that the spatial variability of species richness over continental spatial scales is strongly correlated with contemporary climate. Assuming that this relationship between species richness and climate persists under conditions of increased $CO_2$, what changes could we expect to occur in terms of species richness? To address this question, I used observed relationships between contemporary richness and climate, coupled with climate projections from five GCM, to project these future changes. These models predict that the richness of vertebrate ectotherms will increase over most of the conterminous United States. Mammal and bird richness are predicted to decrease in much of the southern US and to increase in cool, mountainous areas. Woody plant richness is likely to increase throughout the North and West and to decrease in the southwestern deserts. These projections represent changes that are likely to occur over long time scales (millennia); short-term changes are expected to be mainly negative.

**Key words:** diversity; species richness; trees; mammals; amphibians; reptiles; climate change.

## INTRODUCTION

Species richness—that is, the number of species that co-occur in a defined area—varies tremendously over broad spatial scales. In the conterminous United States, for example, tree species richness in 2.5° × 2.5° quadrats varies from 18 species in eastern New Mexico and western Kansas to 181 species in western South Carolina (Currie and Paquin 1987). Mammal species richness ranges from 43 species in northern Maine to 94 in west central California. Reptile richness varies from eight in northern Maine to 86 in southern Texas (Currie 1991).

This variation in richness is strongly related to variation in climate. Temperature and water availability account for more than 75% of the variability in plant species richness over broad spatial scales (Wright 1983; Currie and Paquin 1987; Adams and Woodward 1989; O'Brien 1993). The richness of most terrestrial animal groups, including vertebrates (Currie 1991) and insects (Turner and others 1987; Kerr and others 1998), covaries even more strongly with energy-related variables such as temperature, potential evapotranspiration, and incident solar radiation.

Although the mechanisms that link variations in richness to climate are not clear, several have been proposed (Hutchinson 1959; Brown 1981; Root 1988; Wright and others 1993). However, if climate per se determines broad-scale patterns of richness (as opposed to being simply an indirect correlate thereof: [see Brown 1981, Wright and others

1993]), then changes in climate would be expected to lead to changes in richness. The distributions of individual species have shifted markedly since the end of the last glacial period (Huntley and Birks 1983; Prentice and others 1991). As the climate warmed and patterns of precipitation changed, many species migrated northward (Davis 1981; Pielou 1991). Patterns of species richness also changed as a result of climatic warming. Although species richness does not appear to have kept pace with climatic change during the late Pleistocene and early Holocene, it did change in the directions one would predict, given contemporary richness-climate models and the observed changes in paleoclimate (D. Murray and D. J. Currie unpublished).

What would be the consequences of changes in richness due to changing climate? In experimental systems, species richness has been related to system functioning (Naeem and others 1994, 1995) and to the rate at which ecosystems recover from perturbations (Tilman and Downing 1994; Chapin and others 1998). At broader scales, species extirpations should occur in areas where climate change is predicted to lead to decreases in richness, whereas invasions would occur in areas where richness is predicted to increase. Specific consequences of changing species richness are impossible to predict. Yet clearly, wherever conditions favor large changes in richness, communities can be expected to undergo major reorganization. The protection of rare species or representative ecosystems now extant in these areas will be particularly problematic.

How, then, could we expect broad-scale patterns of species richness to change in response to future climate changes? In particular, if atmospheric $CO_2$ continues to increase dramatically over the next decades, and if global climate changes as predicted by general circulation models (GCM), how would richness change in response? To address this issue, I examined the predictions of several GCM regarding the changes in climate that would be expected to occur in the conterminous United States in response to a doubling of atmospheric $CO_2$. These predicted climate changes were used to project expected changes in the species richness of trees and terrestrial vertebrates.

## METHODS

Contemporary patterns of species richness were generated by superimposing published maps of the geographic ranges of all of the indigenous species of trees, mammals, birds, reptiles, and amphibians in the conterminous US on a 2.5° × 2.5° grid. In each grid cell, I tallied the total numbers of species in each of these groups (Currie and Paquin 1987; Currie 1991).

I then related contemporary patterns of richness to contemporary climate using multiple regression models. Contemporary climate data were drawn from climatic atlases (Currie and Paquin 1987). Because earlier work had shown that patterns of richness were most closely related to measures of heat and precipitation, I restricted the present analyses to those two aspects of climate (specifically, mean January and July temperature and precipitation).

Species richness data were transformed (square root to fourth root) to stabilize the residual variance in statistical models. January precipitation was log transformed and July precipitation square root transformed to make their distributions approximately normal. The resulting relationships between richness and the climatic variables were not always linear. In these cases, I fitted second-degree polynomial regressions. Higher-order polynomial terms were not necessary.

Next, I examined the changes in temperature and precipitation predicted to result from a doubling of atmospheric $CO_2$ ($CO_2 \times 2$) The predictions of the following five GCM were used: the Canadian Climate Centre high-resolution GCM model (Boer and others 1992), the Geophysical Fluid Dynamics Laboratory R30 high-resolution model (Mitchell and others 1990; Cubasch and Cess 1990), the Goddard Institute for Space Studies model (Hansen and others 1984), the Oregon State University model (Schlesinger and Zhao 1989), and the UK Meteorological Office low-resolution model (Wilson and Mitchell 1987). For each of these models, predictions of monthly temperature and precipitation had been derived on a 0.5° grid covering the conterminous US (Melillo and others 1995). The predicted climatological data and further details regarding the GCM are available at http://www.cgd.ucar.edu/vemap/index.html. For each model, I extracted predicted January and July temperature and precipitation for the $CO_2 \times 1$ (current) and the $CO_2 \times 2$ scenarios.

Based on the observed statistical relationships between contemporary richness and climate, plus the GCM climate data, I calculated the predicted richness given the $CO_2 \times 1$ and the $CO_2 \times 2$ scenarios for each cell in the VEMAP grid. I then calculated the ratio of richness for $CO_2 \times 2$, compared to that for $CO_2 \times 1$. Note that the VEMAP grid (0.5° × 0.5° cells) was finer than the grid for the richness data (2.5° × 2.5° cells). Because total observed richness typically increases as a function of the area sampled, richness in 2.5° grid cells is probably greater than that in 0.5° cells. However, I assume in this analysis
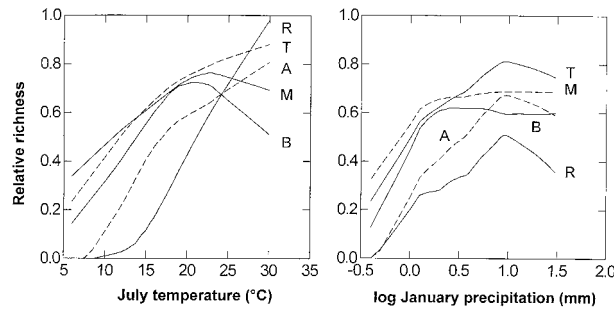
**Figure 1.** The relationships between species richness and January precipitation and July temperature. The curves represent LOWESS curves (locally weighted sums of squares: a robust regression technique that shows trends in data without specifying a mathematical model) fitted to 337 observations of richness and temperature or precipitation in 2.5° × 2.5° quadrats covering North America (Currie and Paquin 1987). Curves for species richness of trees (T), birds (B), mammals (M), reptiles (R), and amphibians (A) are shown. In each case, richness has been normalized to the maximum number of species observed in a quadrat anywhere on the continent. Relationships between richness and January temperature (not shown) are very similar to those with July temperature. Relationships between richness and July precipitation are weak.



**Figure 2.** The relationship between tree species richness (fourth root transformed) and January precipitation and July temperature. Isopleths show a smoothed surface, fitted with diagonally weighted least squares (DWLS), indicating the fourth root of tree species richness. Note that richness increases strongly with temperature at July temperatures less that approximately 20°. At higher temperatures, richness depends strongly on precipitation.

that the ratio of richness estimated under two different climate scenarios would not depend upon cell size at these scales.

## RESULTS

Contemporary patterns of species richness covary strongly with both temperature and precipitation. For most groups of terrestrial organisms, richness increases with temperature and either plateaus or decreases at the highest contemporary temperatures (January temperature is shown in Figure 1; the patterns are very similar for July temperature and mean annual temperature). Richness also generally increases with winter (Figure 1) and total annual precipitation, sometimes declining at the highest levels of precipitation. Relationships with July precipitation (not shown) are more variable. For trees (Figure 2), amphibians, birds, and mammals (not shown), there is a strong interaction between temperature and precipitation: richness covaries strongly with temperature in cool areas of the US (July temperatures less than 20°C) and with precipitation in warmer areas. Precipitation has little effect on reptile richness. These patterns are consistent with richness-climate relationships observed globally (Adams and Woodward 1989; A. Francis and D. J. Currie unpublished).
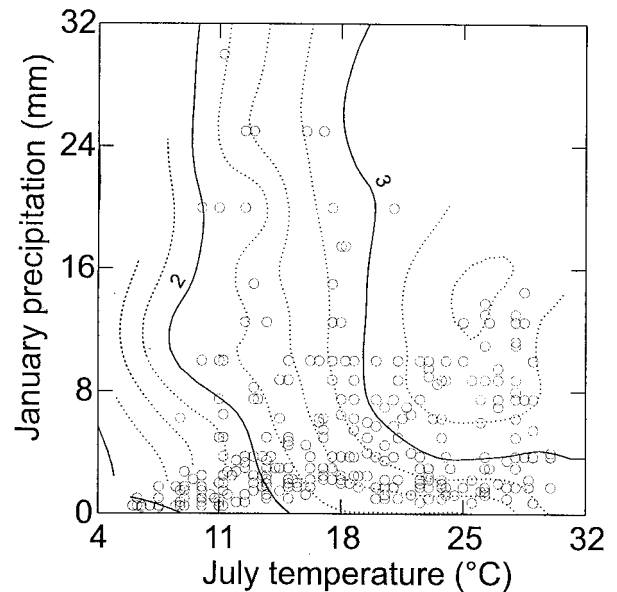
Multiple regression models involving temperature and precipitation account statistically for 83%–94% of the contemporary North American variation in species richness in trees and terrestrial vertebrates (Table 1). For trees and all vertebrate classes, richness is most strongly related to July temperature. All groups also show relationships with precipitation, but the details vary among groups.

On average, general circulation models predict that a doubling of atmospheric $CO_2$ should lead to increases in January temperatures from 3° to 7°C, with the largest changes in the Northeast. Summer temperatures are also predicted to increase, albeit less than the winter temperatures (Figure 3). Much of the Southeast is predicted to become drier, while increases of precipitation are predicted in the Northwest during the winter and in a few spots in the South during the summer.

Using the relationships between richness and climate derived above, we can predict how species richness would be expected to change, given the climate changes expected to result from a doubling of atmospheric $CO_2$. Because different GCM make different predictions regarding climate, the predicted patterns of richness also differ, depending

**Table 1.**  The Standardized Coefficients of the Variables Included ($P < 0.05$) in Multiple Regressions to Predict Species Richness of Trees, Birds, Mammals, Reptiles, and Amphibians

| Variables | Trees$^{0.25}$ | Birds | Mammals$^{0.5}$ | Reptiles$^{0.5}$ | Amphibians$^{0.33}$ |
|---|---|---|---|---|---|
| Jan. temp. | | | — | 0.38 | −0.15 |
| Jan. temp.$^2$ | | −0.44 | −0.37 | | −0.11 |
| July temp. | +1.71 | +2.86 | +2.23 | — | +1.67 |
| July temp.$^2$ | −1.02 | −2.44 | −1.71 | +0.67 | −0.83 |
| log(Jan. precip.) | +0.32 | −0.10 | | −0.15 | — |
| [log(Jan. precip.)]$^2$ | | | | +0.091 | +0.25 |
| July precip.$^{0.5}$ | +0.064 | — | −0.30 | — | — |
| July precip. | | −0.21 | | −0.046 | +0.10 |
| Model $R^2$ | 0.88 | 0.83 | 0.84 | 0.94 | 0.92 |

*Species richness was transformed (square root to fourth root) to stabilize residual variance. Independent variables included January and July temperature and precipitation. Precipitation was transformed (log or square root) to make its distribution approximately normal. As many of the relationships were nonlinear, polynomial terms were used. The magnitude of the standardized coefficient is a measure of the strength of the effect of the independent variable. Thus, richness depends most strongly on July temperature for all of the groups of organisms. For trees, birds, mammals, and amphibians, the positive coefficient on the linear term for July temperature, followed by a negative coefficient on the quadratic term, means that richness initially increases with increasing temperature, but that the relationship decelerates. Eventually, richness reaches a maximum and then begins to decrease. In contrast, reptile richness increases monotonically with increasing temperature.*
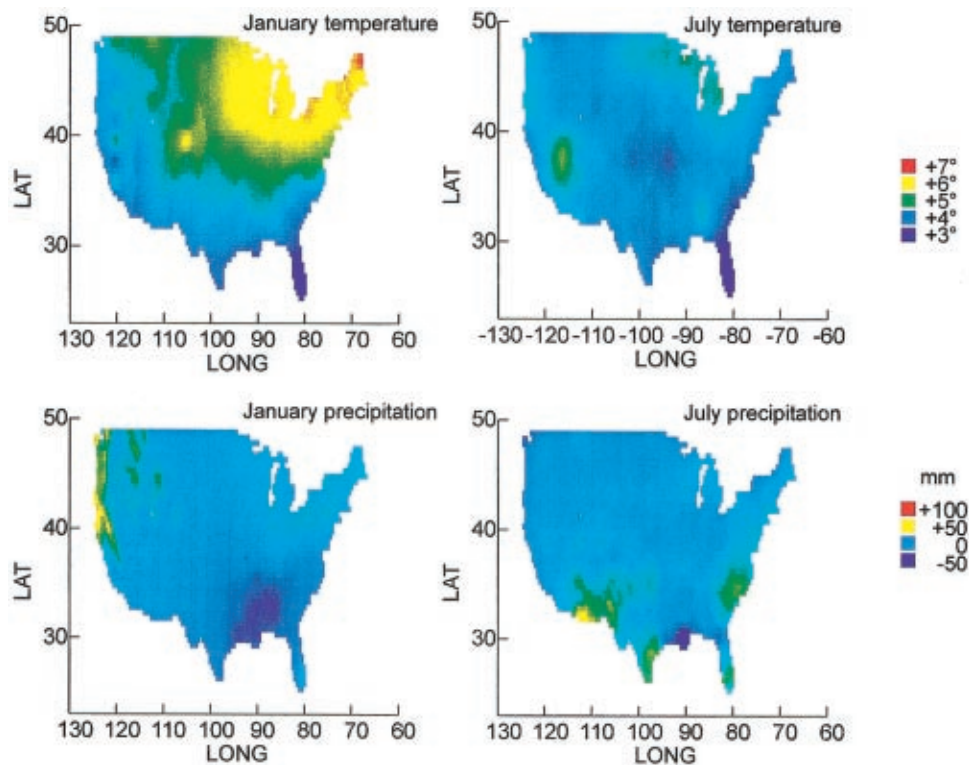


**Figure 3.** The predicted change in January temperature and precipitation and July temperature and precipitation, given doubling of atmospheric $CO_2$, averaged over five general circulation models. Data are expressed relative to the current climate.

upon the GCM used (for example, for trees: Figure 4). The predictions of the GCM are very similar for some regions of the US, and they differ strikingly in others. I therefore calculated an expected response averaged over all five models, as well as a measure of the variability among the five models (Figures 5–9).

According to this analysis, climate change should lead to variable changes in tree richness across the conterminous United States. Little change (less than 10%) in tree richness would be expected in most of the central and southeastern US (Figure 5), although model predictions about northern Florida are quite variable. Large increases are predicted in the Pacific Northwest and the northern Rockies, mainly because of predicted increases in summer temperature. Disagreement among models in the Northwest is mainly at the level of how extensive the increases will be. Significant decreases in tree richness are predicted for the deserts of the South-
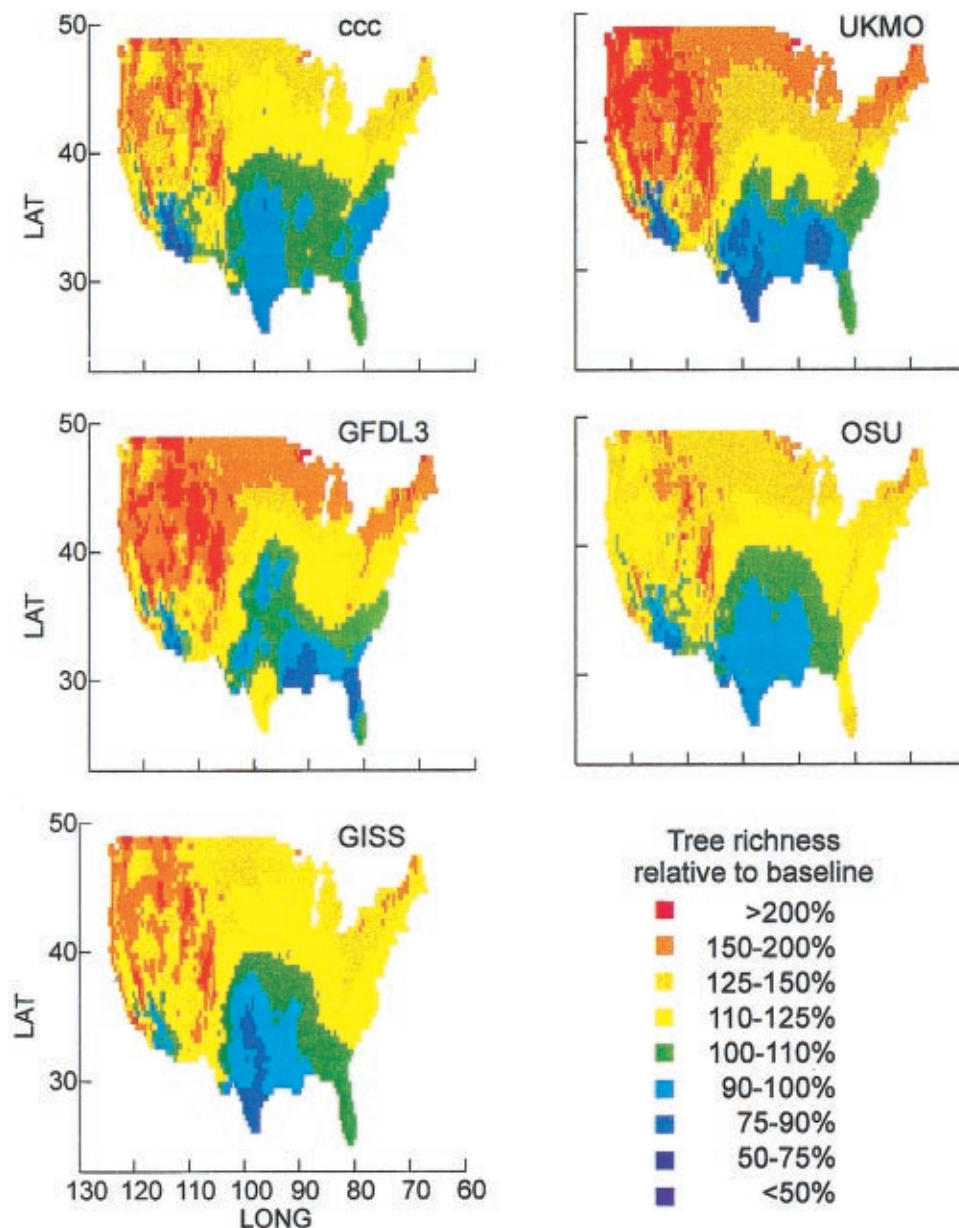
**Figure 4.** Changes in tree species richness, relative to the current richness, resulting from the climatic changes associated with doubling of atmospheric $CO_2$. These predictions were made using five different general circulation models: the Canadian Climate Centre high-resolution GCM model (CCC), the Geophysical Fluid Dynamics Laboratory R30 high-resolution model (GFDL), the Goddard Institute for Space Studies model (GISS), the Oregon State University model (OSU), and the UK Meteorological Office low-resolution model (UKMO).

west associated with the very high summer temperatures. There is little disagreement among GCM on this point.

Bird richness is predicted to be severely affected by climate change (Figure 6) because bird richness, more than that of any other group, tends to be lower in hot areas. Higher temperatures over most of the central and southern US should therefore be accompanied by decreases in bird richness, except at higher elevations. Increases in richness are likely to occur in cooler, high-elevation areas, particularly in the western US.

Mammal richness is predicted to change in much the same way as bird richness (Figure 7), presumably because the richness of the two classes covaries with temperature and precipitation in very similar ways.

Contemporary reptile richness increases monotonically with temperature (Figure 1). Climatic warming should be very positive for reptiles (Figure 8), with large increases in richness predicted over the northern half of the US.

Amphibian richness is similarly positively related to July temperatures. However, amphibian richness is more strongly related to precipitation than reptile richness. Amphibian richness, while predicted to increase nearly everywhere in the conterminous US, is likely to change most dramatically in cold; high-elevation areas (Figure 9).

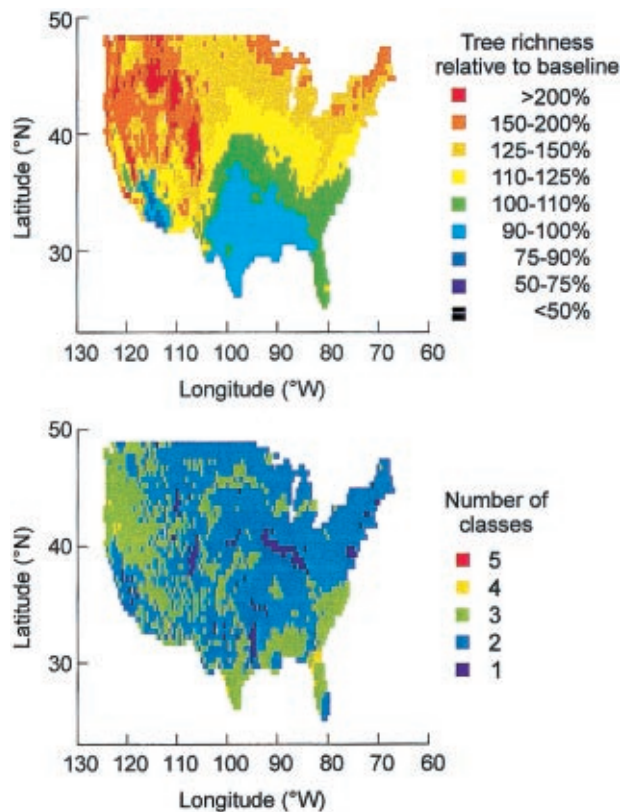Note that several of the predicted changes in

**Figure 5.** Changes in tree species richness, relative to the current richness, resulting from the climatic changes associated with doubling of atmospheric $CO_2$. Richness was projected using five general circulation models (GCM). The average richness, categorized into nine classes, is shown here (*top*). The variance among GCM is indicated by showing the number of different classes predicted by the five GCM (*bottom*). Thus, areas in which all GCM predicted richness changes in the same class are indicted as having one class; two classes indicates that two different classes are predicted among the five GCM, and so on.

**Figure 6.** Changes in bird species richness, relative to the current richness, resulting from the climatic changes associated with doubling of atmospheric $CO_2$. Richness was projected using five general circulation models (GCM). The average richness, categorized into nine classes, is shown here (*top*). The variance among GCM is indicated by showing the number of different classes predicted by the five GCM (*bottom*).

climate lead to temperature or precipitation levels that are outside the range of variables in the contemporary calibration data set (Figure 10). The extremes in predicted precipitation levels are only slightly outside those observed currently in the US. The hottest predicted July temperatures, however, exceed the hottest July temperatures now observed by as much as 4°C in areas of the Southwest and southern Texas. Predicted changes in richness in these areas may therefore be suspect.

## DISCUSSION

It is well documented that broad-scale patterns of species richness are most strongly and consistently related to climate variables that are plausibly related
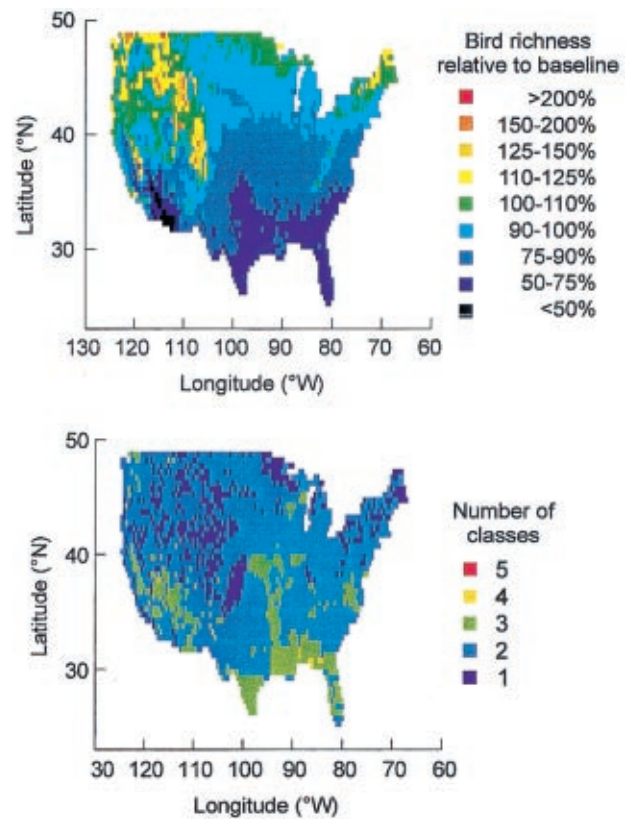
to organisms' productivity and energy balance (Wright and others 1993). The mechanism is unknown. Although the climatic tolerances of individual species may limit their geographic distributions (Root 1988), patterns of richness appear to be determined by more than simply the tolerances of individual species because the number of species that can tolerate the environmental conditions in any given place is usually much greater than the number that actually occur there (Cornell 1985; Cornell and Karlson 1996). Hutchinson (1959) and others (Brown 1981; Currie 1991) have proposed that available energy sets a cap on the maximum number of species that can co-exist in a region. Available energy limits richness, in some sense. Several of my collaborators (including J. T. Kerr and A. Francis) and I are currently exploring the possibility that climatic variables may actually influence the diversity of microhabitats that are, in practice,
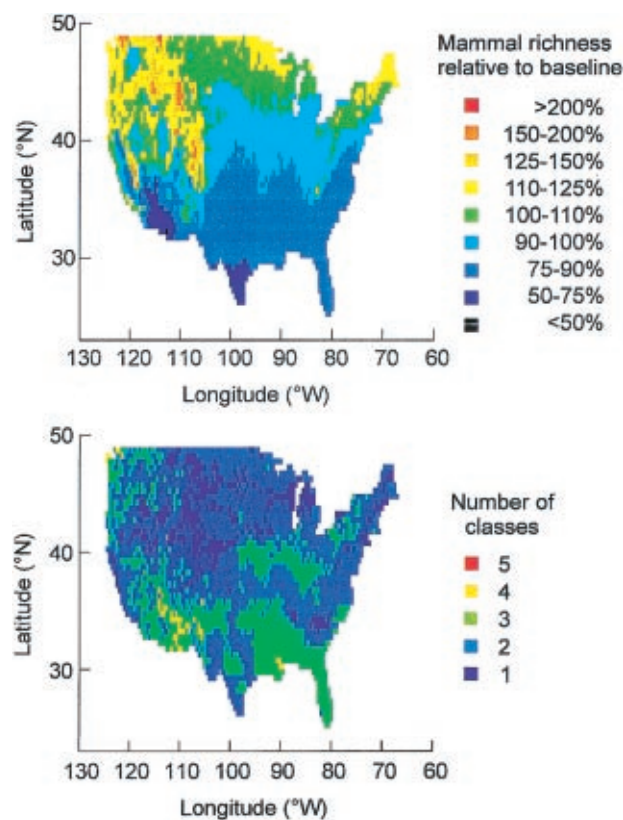
**Figure 7.** Changes in mammal species richness, relative to the current richness, resulting from the climatic changes associated with doubling of atmospheric $CO_2$. Richness was projected using five general circulation models (GCM). The average richness, categorized into nine classes, is shown here (*top*). The variance among GCM is indicated by showing the number of different classes predicted by the five GCM (*bottom*).

**Figure 8.** Changes in reptile species richness, relative to the current richness, resulting from the climatic changes associated with doubling of atmospheric $CO_2$. Richness was projected using five general circulation models (GCM). The average richness, categorized into nine classes, is shown here (*top*). The variance among GCM is indicated by showing the number of different classes predicted by the five GCM (*bottom*).

available in a region. Under both hypotheses, climate has a direct limiting effect on richness.

It has also been well documented that major shifts in species' distributions, as well as extinction of some taxa, followed the climate changes at the end of the last glacial period (Pielou 1991). It is reasonable to expect that changes would also occur if enrichment of the atmosphere with greenhouse gases were to lead to substantial changes in temperature and precipitation in the future. But how great are these changes likely to be, and where are they likely to occur?

I believe that the results presented here represent estimates of the potential species richness toward which observed richness would move over very long periods. In other words, I doubt that Figures 5 to 9 represent actual levels of richness that will be observed; rather, they represent estimates of the steepness of the gradient along which richness is
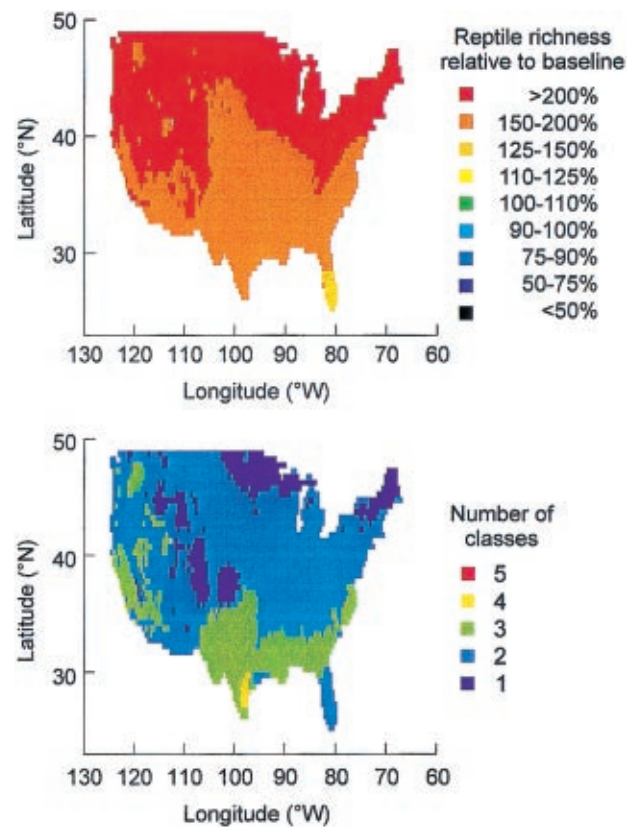
predicted to change in the long term. Other work (D. Murray and D. J. Currie unpublished) has suggested that changing patterns of richness during the Holocene and late Pleistocene failed to keep pace with climate change, although the changes in richness were in the direction predicted by our contemporary richness–climate relationships. Because changes in climate in the future could be even more rapid, it is very unlikely that richness would track them.

It is quite possible that over the short term (decades to centuries) species richness will decrease, even in areas where richness is predicted to increase in the long term. As climate changes, species that are intolerant of local conditions may disappear relatively quickly. In contrast, migration of new species into the area may be quite slow (Davis 1984).

Over much of the conterminous US, predictions about changes in richness are qualitatively similar,
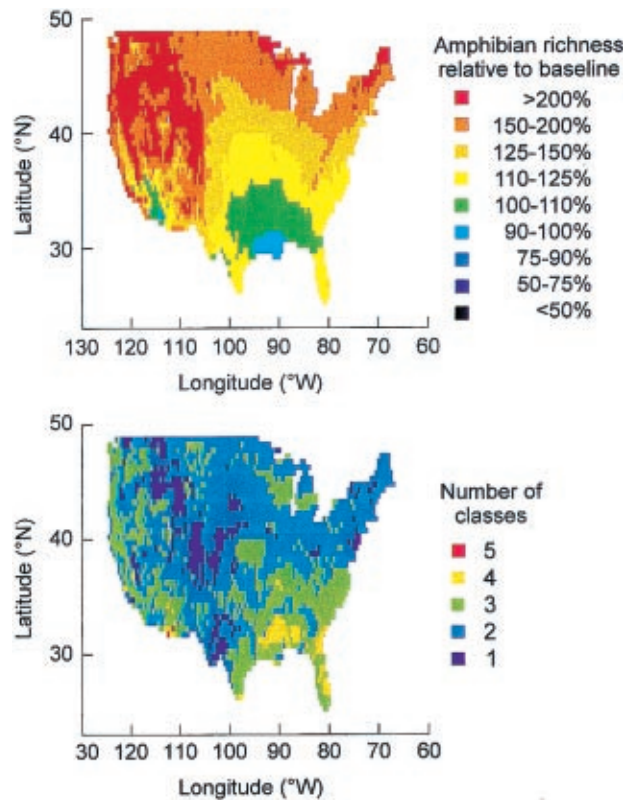
**Figure 9.** Changes in amphibian species richness, relative to the current richness, resulting from the climatic changes associated with doubling of atmospheric $CO_2$. Richness was projected using five general circulation models (GCM). The average richness, categorized into nine classes, is shown here (*top*). The variance among GCM is indicated by showing the number of different classes predicted by the five GCM (*bottom*).

**Figure 10.** Areas in which January or July temperature or precipitation are predicted by at least one general circulation model (GCM) to fall outside the range currently observed (*top*). Also shown is the number of times this occurs out of 20 possible simulations (four variables × five GCM).

irrespective of the GCM used to project climate, and extrapolation beyond contemporary richness–climate relationships is not necessary. Thus, those predictions depend little on the assumptions of particular climate models. However, in the southwestern deserts, in southern Texas, and along the East Coast from the Carolinas to the Florida Keys there is significant disagreement among climatic models. Worse, predicted climates often fall outside the contemporary range of climate variables in these areas. Extrapolation of contemporary richness–climate relationships beyond the conditions under which they were derived seems risky, particularly since the relationships between richness and climate are nonlinear.

Predictions in mountainous areas are probably exaggerated. Climate averaged over 0.5° cells (which were used for the climate projections) can reach more extreme values than it does in 2.5° cells (which were used to calibrate richness and climate),
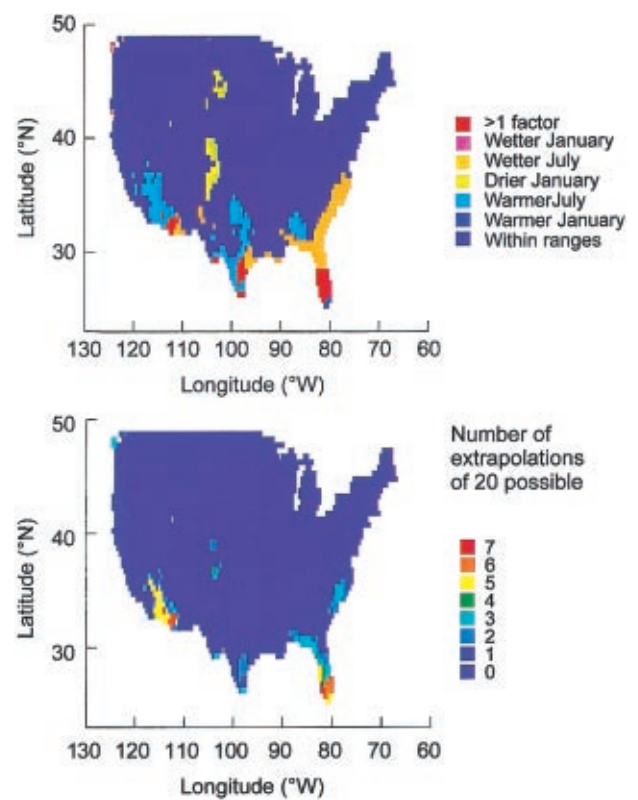
especially in topographically heterogeneous areas. Thus, it is likely that the predicted changes are overestimated in mountainous areas. I would not expect scale effects to be perceptible in areas that are topographically more uniform.

The results presented here are predictions derived from models (that is, from hypotheses). In other words, model outputs represent what would occur if the premises of the models were strictly correct. The most important premise in this study is that the pattern of covariation between richness and climate, and the covariation among climate variables, will not change as climate changes. Our work on climate and richness during the Holocene is consistent with this premise. However, future climate changes may be qualitatively very different than past ones, and the only true way to test the present models is to observe what happens when atmospheric $CO_2$ doubles.

Mechanistic models (vs the purely correlative ones presented here) offer an alternative approach to forecasting the effects of climate

change. Such models could incorporate the extensive experimental results that have shown how, under controlled conditions, increased $CO_2$ and temperature can affect processes such as carbon allocation, growth, seed production, herbivory, and competitive relationships (for example, Pacala and Hurtt 1993). Yet mechanistic models also rely upon a troublesome premise: that the mechanisms thought to be important today will continue to be the main driving variables after climate changes, and that no other variable not included in the model will become important. Even a detailed knowledge of mechanisms does not guarantee that patterns in nature can be predicted (for a dramatic example, see Chitty 1996). In practice, the definitive test of all climate change projections relies upon observing what happens when climate actually changes. The present results also depend upon assumptions inherent in the general circulation models.

In conclusion, although it cannot be known definitely how species richness will change if atmospheric $CO_2$ doubles, the present results suggest that marked increases in the richness of most taxa are likely to occur in cool regions, while decreases in homeotherm richness are likely to occur in parts of the South.

## ACKNOWLEDGMENTS

## REFERENCES

Adams JM, Woodward FI. 1989. Patterns in tree species richness as a test of the glacial extinction hypothesis. Nature 339:699–701.

Boer GJ, McFarlane NA, Lazare M. 1992. Greenhouse gas–induced climate change simulated with the CCC second-generation general circulation model. J Clim 5:1045–77.

Brown JH. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. Am Zool 21:877–888.

Chapin FS III, Sala OE, Burke IC, Grime JP, Hooper DU, Laurenroth WK, Lombard A, Mooney H, Mosier AR, Naeem S, Pacala SW, Roy J, Steffen W, Tilman D. 1998. Ecosystem consequences of changing biodiversity. BioScience 48:42–52.

Chitty D. 1996. Do lemmings commit suicide? Beautiful hypotheses and ugly facts. New York: Oxford University Press.

Cornell HV. 1985. Species assemblages of cynipid gall wasps are not saturated. Am Nat 126:556–569.

Cornell HV, Karlson RH. 1996. Species richness of reef-building corals determined by local and regional processes. J Animal Ecol 65:233–241.

Cubasch U, Cess RD. 1990. Processes and modeling. In: Houghton, JT Jenkins GJ, Ephraums JJ, editors. Climate change: the IPCC scientific assessment. Cambridge (UK): Cambridge University Press. p 69–91.

Currie DJ. 1991. Energy and large scale patterns of animal and plant species richness. Am Nat 137:27–49.

Currie DJ, Kerr JT, Francis AP. 1999. Some general propositions about the study of spatial patterns of species richness. Ecoscience. 6:392–399.

Currie DJ, Paquin V. 1987. Large-scale biogeographical patterns of species richness in trees. Nature 329:326–27.

Davis MB. 1984. Climatic instability, time labs, and community disequilibrium. In: Diamond J, Case TJ, editors. Community ecology. New York: Harper & Row. p 269–84.

Davis MB. 1981. Quaternary history and the stability of plant communitites. In: West DC, Shugart HH, Botkin DB, editors. Forest Succession: concepts and application. New York: Springer-Verlag. p. 132–53.

Hansen J, Lacis A, Rind D, Russell G, Stone P, Fung I, Ruedy R, Lerner J. 1984. Climate sensitivity: analysis of feedback mechanisms. p 130–63. In: Hansen JE, Takahashi T, editors. Climate Processes and Climate Sensitivity. American Geophysical Union, Washington, D.C.

Huntley B, Birks HJB. 1983. An atlas of past and present pollen maps for Europe: 0–13000 years ago. Cambridge (UK): Cambridge University Press.

Hutchinson GE. 1959. Hommage to Santa Rosalia, or why are there so many kinds of animals? Am Nat 93:145–59.

Kerr, JT, Vincent R, Currie DJ. 1998. Lepidopteran richness patterns in North America. Ecoscience 4:448–453.

Meilillo JM, Borchers J, Chaney J, Fisher H, Fox S, Haxeltine A, Janetos A, Kicklighter DW, Kittel TGF, McGuire AD, McKeown R, Neilson R, Nemani R, Ojima DS, Painter T, Pan Y, Parton WJ, Pierce L, Pitelka L, Prentice C, Rizzo B, Rosenbloom NA, Running S, Schimel DS, Sitch S, Smith T, Woodward I. 1995. Vegetation/Ecosystem Modeling and Analysis Project (VEMAP): Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and $CO_2$ doubling. Global Biogeochem Cycles 4:407–437.

Mitchell JFB, Manabe S, Meleshko V, Tokioka T. 1990. Equilibrium climate change and its implications for the future. In: Houghton JT, Jenkins GJ, Ephraums JJ, editors. Climate change: the IPCC scientific assessment. Cambridge (UK): Cambridge University Press. p 131–72.

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368:734–7.

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. Philos Trans R Soc London [B] 347:249–62.

O'Brien EM. 1993. Climatic gradients in woody plant species richness—towards an explanation based on an analysis of southern Africa's woody flora. J Biogeog 20:181–98.

Pacala SW, Hurtt GC. 1993. Terrestrial vegetation and climate change: integrating models and experiments. In: Kareiva PM, Kingsolver JG, Huey RB, editors. Biotic interactions and global change. Sunderland (MA): Sinauer Associates. p 57–74.

Pielou C. 1991. After the ice age. Chicago: University of Chicago Press.

Prentice IC, Bartlein PJ, Webb TI. 1991. Vegetation and climate

clange in eastern North America since the last glacial maximum. Ecology 72:2038–56.

Root T. 1988. Energy constraints on avian distributions and abundances. Ecology 69:330–9.

Schlesinger ME, Zhao ZC. 1989. Seasonal climate changes induced by doubled $CO_2$ as simulated by the OSU atmospheric GCM–mixed layer ocean model. J Clim 2:459–495.

Turner JR, Gatehouse CM, Corey CA. 1987. Does solar energy control organic diversity? Butterflies, moths and the British climate. Oikos 48:195–205.

Wilson CA, Mitchell JFB. 1987. A doubled CO2 climate sensitivity experiment with a global climate model including a simple ocean. J Geophys Res 92:13315–43.

Wright DH. 1983. Species–energy theory: an extension of species–area theory. Oikos 41:496–506.

Wright DH, Currie DJ, Maurer BA. 1993. Energy supply and patterns of species richness on local and regional scales. In: Ricklefs RE, Schluter D, editors. Species diversity in ecological communities: historical and geographical perspectives. Chicago: University of Chicago Press. p 66–74.